PRINCIPLES OF PLANT TAXONOMY. I.*

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In 1905, the writer began publishing a series of papers on the phyletic classification of plants, which gave a general arrangement of the entire plant kingdom and also a discussion, in an elementary way, of the evolutionary facts on which a true classification must ultimately rest. These papers appeared in THE OHIO NATURALIST and its continuation as THE OHIO JOURNAL OF SCIENCE. No. I appeared in Vol. V, 1905; Nos. II and III in Vol. VI, 1905–6; Nos. IV and V in Vol. IX, 1909; Nos. VI and VII in Vols. XI and XII, respectively, 1911; Nos. VIII, IX, X and XI, in Vols. XIII and XIV, 1913; and No. XII, after a long hiatus, in Vol. XXII, 1922.

It is now the intention to publish a new series with special emphasis on the facts which appear to be of importance in determining a correct, evolutionary arrangement and phylogenetic classification. Some of the material given in the previous papers will not be repeated, but some of it will be considered and restated in the light of a more complete knowledge of plants, acquired by the writer through his own efforts and those of other investigators. The subjects treated will be taken up more or less at random, sometimes presenting a general aspect of the subject and sometimes a special case considered in detail.

THE SEVEN FUNDAMENTAL DIVISIONS OR SUBKINGDOMS.

In order to obtain a correct background for any scheme of classification, it is of the grestest importance to discover what have been the main movements and evolutionary advancements that have taken place in passing from the lowest to the highest types. Without reference to any notion of phyletic relationship, what is the general nature of the various types of higher and higher plants as one takes a general view of the whole plant kingdom? Such a view presents seven definitely marked stages

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or subdivisions, no more and no less; and each higher division is characterized by the acquisition of fundamentally new properties and activities, which result in new complexities in the life cycle, physiological processes, and structures. At each of the six transition stages some fundamental property or relation is added which is retained, after that, throughout all succeeding stages and is very rarely lost in individual cases. The emphasis will be placed on fundamental processes and physiological relations rather than on structures, as has usually been done, for it has become plain that the structures developed in any individual result from the presence of hereditary factors through the physiological activities of the cells in the given environment. In placing the emphasis on fundamental properties and functions, our classification will appear in a clearer light as simply a systematizing of the evolutionary progressions. and a more or less correct chronological arrangement of the more and more complex heredities that result in new activities, interrelations, and structures of cells and organs as one passes up the ladder of organic forms. There are, of course, morphological characteristics which delimit the subkingdoms very distinctly except the two lowest, which are separated on purely physiological grounds, since the lowest sexual forms show no dimorphism even in the gametes. But as stated above, the morphological characters are in the end merely the result of activities dependent on the presence of a given heredity in a given environment, and by emphasizing morphological features in the segregation of the great progressive divisions the attention is diverted from the main point of importance and interest. It is also possible to define the seven subkingdoms entirely in terms of their life cycles. Each group has one or more characteristic life cycles; that will clearly segregate it from all others except in the case of low forms without secondary sexual characters that have lost their sex.

The lowest plants are then apparently without sexuality. The organization of their protoplasts is apparently such that no sexual states arise under any known conditions. These nonsexual plants include unicellular and colonial forms and multicellular forms with cell differentiation. Some might object to the recognition of these plants as a distinct subkingdom since abundant unicellular forms occur which have well-developed sexual states, but since the upward evolution of the plant kingdom is so intimately associated with changes in the relation of the sexual state to the life cycle, it is necessary from theoretical grounds to lay emphasis on the fact that the first type of living things that appeared on the earth was apparently nonsexual and has so remained. These primitive, nonsexual plants constitute the subkingdom PROTOPHYTA.

In general, plants proceed from the unicellular to the multicellular condition, both in the ontogeny and in the phylogeny, but the transition is so gradual and involves so little change in the functional nature of the organism that it is impossible to separate the unicellular from the multicellular. In fact it is much more difficult to segregate the strictly unicellular from the strictly multicellular than to separate those with sexual states from the non-sexual. The difficulty arises because sexual organisms may fall back into such a condition that no sexual state ever develops.

In the higher forms which have lost their normal sexuality, partial or secondary sexual states arise, but in one way or another the perfect, primary sexual state is not attained and the species continues either parthenogenetically or apogamously. In the lower, unicellular and colonial species it is often difficult or impossible to form a convincing judgment as to whether the organism in question was derived from a previous sexual condition or whether it represents a direct derivative from the original nonsexual state. Such cases must be decided by a study of the complexity of the cell in general and the nucleus, and by a comparison with the nearest relatives. Usually there will be less uncertainty than there is in separating lower "plants" from lower "animals." The other five transitions offer no such difficulties. In fact with an ordinary knowledge of the morphology and life history, every species can be placed with absolute certainty. There are attraction stages in some lower organisms which in physical nature may be somewhat akin to sexuality which, nevertheless, are to be regarded as distinct phenomena not related to sexual states, namely the aggregations, fusions, or associations of cells at certain periods, as manifested in Myxobacteriales, Myxophyta, and Hydrodictyales.

In general, plants proceed from the uncellular through the colonial state to the multicellular condition, with little change in the functional nature of the organism. However, the change from unicellular to multicellular frequently also involves a change from nonsexual to sexual, although these two evolutionary progressions are apparently due to fundamentally distinct causes.

The second subkingdom is named NEMATOPHYTA because of the prevalence of the filamentous condition in most of its classes, and because in the two succeeding subkingdoms the gametophyte usually passes through a protonema stage in its embryogeny. In this subkingdom there are three main types of life cycle: first, a simple sexual cycle with a haploid individual; second, a simple sexual cycle with a diploid individual; and third, an alternation of generations cycle with a haploid individual alternating with a diploid individual, the diploid individual being independent of the haploid individual, although in some cases a diploid, spore producing parasitic phase is present at first as in some red algæ. This alternation cycle is therefore quite distinct from the one which appears in the next higher subkingdom and which remains fundamentally unchanged to the highest plants. Each of the three life cycles of the Nematophyta may be modified in one way or another in details, the most extreme, perhaps, being the modification of the alternation cycle in such higher fungi as the rusts, where the diploid generation consists of cells with pairs of haploid nuclei rather than of cells with diploid sets of chromosomes in conjugated nuclei. Such a condition could arise if the conjugating nuclei lost, for the time being, their primary sexual states or property of attraction before coming in contact and developed it again at the end of the diploid generation stage. In contrast to the diversity of life cycles in the Nematophyta, each of the subsequent subkingdoms has but one general type of life cycle and, as stated above, all are mere modifications of one fundamental type.

The second transition in the plant series is that which leads up to the BRYOPHYTA. This is by far the greatest break or hiatus in the plant kingdom from a morphological point of view, there being no possible direct connection until one passes down to the very simple green algæ of the confervoid type. The higher green algæ have not only a different life cycle, but entirely different sexual organs. The gametangia of the Bryophytes come close in structure to those of certain brown algæ, but there is no possibility of a direct relation with this group. So a series of hypothetical forms must be postulated for the ancestry of the liverworts and mosses. The transition to the Bryophytes marks the change from plants adapted to an aquatic habitat to those adapted to live and thrive in aerial conditions. Many Thallophytes are adapted to endure aerial conditions but usually they can only grow well during very wet periods or in very damp places, except some parasites which are, of course, supplied with moisture by their hosts. The lower types of Bryophytes are not entirely weaned from the aquatic habit, but the higher species usually show a greater and greater modification toward dry-land conditions, which finally becomes the goal of the evolutionary process. All along the line, however, there may be, here and there, a return to a secondary aquatic life. A second characteristic of the third subkingdom is the new type of antithetic alternation of generations with a permanently parasitic sporophyte. This new life cycle with its twelve fundamental, antithetic stages is retained, but evolved into a more complicated succession of intermediate stages, step by step, to the highest plants. Its presence or absence becomes a definite division line for the entire plant kingdom into Thallophytes and Meta-thallophytes. The archegonium is a new type of ovary which is barely hinted at in the Nematophyta, and the development of numerous sporocytes in a special tissue is also characteristic.

The third subkingdom, or BRYOPHYTA, may, therefore, be defined as those plants which have an antithetic alternation of generations and a permanently parasitic diploid sporophyte. The sporophyte is always homosporous. One of the most interesting developments in this subkingdom is the remarkable evolutionary advancement of the sporophyte, which passes from the condition of a simple sporangium or sack of nonsexual spores to a highly specialized individual containing a foot, stalk with a conducting strand of cells, hypophysis with true stomata and photosynthetic tissue, and a highly specialized sporangium; and in one group an intermediate growing zone, which is the first indication of indeterminate growth. Parasitism in this case has certainly not led to degeneration, but has led the way toward a condition of highly organized independent existence. By no possible stretch of the imagination could this series be considered as a reverse evolution.

The third transition, which is also a prominent hiatus, leading to the fourth subkingdom, is the consummation of the development carried forward in the evolution of the Bryophytes, namely, the change from a permanently parasitic sporophyte to a sporophyte with two distinct stages or phases in its life-history, first a juvenile parasitic stage and second a mature independent stage in which roots, true vascular tissue, highly organized leaves, and indeterminate buds are developed. The sporophyte with its indeterminate growth shows an enormous advance over the determinate sporophyte of the Bryophytes. Its early parasitic condition can properly be interpreted as being derived from a completely parasitic condition similar to that of the Bryophytes. The fourth subkingdom, or PTERIDOPHYTA HOMOSPORÆ, may, therefore, be defined as those plants with a typical alternation of generations in which the sporophyte has two distinct stages, a parasitic stage and an independent stage, and which is homosporous, the sexual state being normally determined in some stage of the development of the gametophyte. The life cycle of the Homosporous Pteridophytes, therefore, is essentially the same as in the Bryophytes, except in the peculiarity of the sporophyte having two distinct stages of existence, although the morphology of the sporophyte shows an enormous advance over the previous condition. There is no apparent ancestor among the Bryophytes, although the Anthocerotæ suggest a possible distant relationship to the hypothetical ancestors of the Pteridophytes. All plants above the Bryophytes have sporophytes with the two stages, but in some cases, of course, the second stage may be a parasite on a foreign host.

The fourth transition leading up to the fifth subkingdom is again, like the first transition, especially concerned with the sexual state. The determination of the sexual state is transferred back from the gametophyte or the spores from which the gametophyte originates to the tissues of the sporophyte generation, and as in the original evolution of sexuality, so here also, the transition appears to have occurred in a number of independent groups. Although the gap between the living Heterosporous Pteridophytes on the one hand and the Homosporous Pteridophytes on the other is small, it represents one of the most important and profound changes in the whole evolutionary progression. Below, sex is determined in haploid individuals and above in diploid individuals. It does not seem possible that anything like a seed plant could have evolved without this preliminary step. All plants above this transition are heterosporous and always show some sexual dimorphism in the sporophyte, although in the lowest this dimorphism does not extend beyond the tissues of the sporangium and its stalk. In the extreme cases sexuality is determined in the zygote and thus the entire individual may show secondary sexual dimorphism.

Along with the transfer of the time of sex determination to the sporophyte goes a great reduction in the size and complexity of the gametophyte, which must now, of course, under normal conditions always be unisexual. This extreme reduction naturally leads to the next great transition, the development of seed plants. The PTERIDOPHYTA HETEROSPORÆ may be defined as those seedless plants in which the sexual state is determined in the tissues of the sporophyte and in which the gametophyte is greatly reduced, but is not entirely parasitic on the sporophyte, although there may be a beginning of parasitism in the juvenile stage. The life cycle becomes much more complex since there are now two kinds of sporangia, two kinds of sporocytes, and two kinds of nonsexual spores.

The change from the Heterosporous Pteridophytes to the next higher subkingdom, the GYMNOSPERMÆ, is from independent gametophytes to completely parasitic gametophytes, the spores not being shed. The female gametophyte is permanently parasitic in the megasporangium and the male gametophyte or pollen grain is at first parasitic in the microsporangium and later, on the megasporangium or ovule by means of the pollen-tube. This parasitic pollen-tube is a structure characteristic of all seed plants and along with numerous other peculiarities indicates their high position. So seed plants may be defined as those plants which have a male gametophyte with two distinct parasitic stages. Another fundamental change from the condition in the Homosporous and Heterosporous Pteridophytes is the intercallation of a resting period between the parasitic and independent stages of the sporophyte. From the liverworts on up there are, therefore, three prominent steps in the progressive evolution of the sporophyte. In the Bryophyta, the sporophyte is continuously parasitic and determinate in growth. In the Pteridophyta, the sporophyte has an embryonic parasitic stage followed, through a gradual change, by an independent stage with an indefinite period of growth. In the Spermatophyta, a profound resting period, with a subsequent re-awakening or sprouting, is almost universally developed between the parasitic embryonic stage and the later independent stage of growth.

The typical seed plant has been completely weaned from a free water habit by taking the gametophyte from the ground and by conducting the sperms to the ovaries by means of the pollen tube. The Gymnospermæ are, therefore, the higher plants with parasitic gametophytes in which the male gametophyte falls directly into the micropyle of the ovule during pollination and thus develops a short pollen-tube, since the carpel is open and without a stigma.

It may be noted, in passing, that with the development of the seed and the resting period of the sporophyte embryo, the young sporophyte is largely taken out of the struggle for existence. It is an interesting fact that the highest plants, like the highest animals, have evolved this special care for the young of the next generation. And it is still more wonderful to contemplate all the complex changes in structures and functions that had to take place simultaneously or in close succession, in the evolution of these plants, if the complex arrangement was to work at all.

The sixth transition leading to the final or seventh subkingdom, the ANGIOSPERMÆ, is marked by the closing up of the carpellate leaf and the development of a stigma. Pollination is, therefore, no longer on the micropyle of the ovule but far removed and the pollen-tube is correspondingly long, having an extensive development before reaching the ovule. The second parasitic state of the male gametophyte has become highly perfected. It is interesting to note that among the ferns some groups also chose their leaflets over the sporangia. Since living seed plants were apparently all derived from the ferns it is only natural that there should be both open and closed sporophylls. The gametophytes of Angiosperms hold in general the same relations as those of the Gymnosperms, but are reduced to an extreme degree. A new development also is the process of triple fusion from which a new triploid tissue is produced beside the embryo sporophyte. This endosperm or xeniophyte is not present in the Gymnosperms, although there is occasionally a fusion of the ventral canal cell with the second sperm of the male gametophyte. In a few Angiosperms more than three cells may be concerned in the formation of the initial cell of the xeniophyte. In the Angiosperms, therefore, normally five conjugating cells are in evidence at the fertilization period rather than two, as in other plants. In the Angiosperms which have primarily bisporangiate flowers with the stamens below, there is very commonly a showy perianth produced through the sterilization of the lower stamens. There is also some slight sterilization of basal sporphylls in some of the Gymnosperms, but this is never very prominent.

The transition to the Angiospermæ represents an enormous gap. There is apparently nothing so far known to indicate the line of ascent from their probable ancestors, the eusporangiate ferns. The Angiospermæ do not have any direct relation to any of the Gymnospermæ unless perhaps the Pteridospermæ. But the Pteridospermæ seem rather to be in the direct line leading up to the Cycads, Cordaites and Ginkgoes.

These then are the fundamental steps in the ladder of ascent in the plant kingdom. There are seven stages, no more and no less; for although in each of the seven subkingdoms there is a progressive advancement, this does not at any point involve a fundamental departure from established structures and functions taken by all the members, but rather a gradual advancement taken in one or more lines in the subkingdom and not marking a distinct or abrupt transition from lower to higher.

All of the higher plants are flowering plants, namely, they have their sporophylls developed on determinate axes, but the change from flowerless plants with indeterminate sporophyll-bearing axes to flowering plants takes place at entirely different levels in different groups. In lycopods and horsetails the strobilus is attained in the homosporous state. Apparently none of the ferns, either eusporangiate or leptosporangiate, and none of the quillworts evolved determinate sporophyll axes, and in the Cycadophyta the seed habit was well advanced before flowers appear. There are still two living genera of seed plants which show a flowerless condition and there is no plausable reason for supposing that they were ever any different in this respect.

In Ginkgo, neither stamens nor carpels are produced on determinate axes, although some interpret the single stamen and the single carpel as highly reduced strobili. But the latter view has little weight, for practically all the evidence points unmistakably in the other direction. In Cycas the determinate axis is a sex limited character, being developed only in plants in the male state, the carpels being produced in rosettes on the indeterminate main axis of the carpellate plant.

In the broadest sense, therefore, the presence and absence of the flower does not form a basis for grouping the higher plants into primary divisions, although after it once gets well started along the evolutionary pathway, it becomes an organ of decided progressive and segregative tendencies. It might be added that fundamentally the higher types of flowers do not differ from the lower, although as the term is popularly applied it might be inferred that Angiosperms have "flowers" and other plants do not. But there is no basis for such a notion unless the flower is defined in purely arbitrary terms.

To summarize, the evolution of the seven fundamental stages is as follows:

1. The lowest plants are non-sexual.

2. The change to the second stage is the evolution of the cell to a condition that sexual states appear from time to time, giving rise to cell conjugations and three general types of life cycles.

3. The second transition is to plants with a typical, antithetic alternation of generations life cycle with twelve fundamental stages, and with a permanently parasitic, determinate, homosporous sporophyte.

4. The third transition is to plants with a similar life cycle but having a homosporous sporophyte of indeterminate growth with two distinct stages of existence, a parasitic juvenile stage followed by an independent mature stage with roots, leaves and vascular tissue.

5. The fourth transition is to plants which have their sexual states determined in the sporophyte which thus develops, in distinct dimorphic sporangia, male producing microspores and female producing megaspores. There is also a decided tendency toward extreme reduction of the gametophyte.

6. The fifth very pronounced transition is to plants which have parasitic gametophytes, the male gametophyte having a two-phased parasitic life, the first stage in the microsporangium and the second in the megasporangium by means of the pollen tube. The sporophyte has a resting stage intercallated between its parasitic and independent phases. In the subkingdom immediately above the transition the transfer of the pollen (pollination) is directly to the micropyle of the ovule and there is no xeniophyte or true endosperm developed.

7. The sixth transition is to the highest plants with a specially developed structure, the stigma, for the reception of the pollen or male gametophyte, because of the closing up of the carpel. In consequences of this a long pollentube is developed which finally grows into the ovule. The gametophytes show the most extrement reduction and there are typically five cells concerned in conjugations during the fertilization period, a male and a female cell uniting, as in the plants below this stage, to form the initial cell of the diploid sporophyte, and a male cell and normally two cells from the female gametophyte uniting to form the initial cell of the xeniophyte or triploid endosperm. Probably universally, by a sterilization of stamens, a perianth is produced, which may be lost again through reduction.

The seven subkingdoms which form the foundation on which all plant classification must be constructed are, therefore, the following.

VII. ANGIOSPERMÆ.
VI. GYMNOSPERMÆ.
V. PTERIDOPHYTA HETEROSPORÆ.
IV. PTERIDOPHYTA HOMOSPORÆ.
III. BRYOPHYTA.
II. NEMATOPHYTA.
I. PROTOPHYTA.

THE CLASS.

As shown in the discussion above, the seven subkingdoms or divisions do not represent natural or phyletic groups. In only two cases is there any direct connection between members of a lower subkingdom and those immediately above and both these transitions are in relation to the determination of sexual states. It is because of their sharp demarkation from each other that the subkingdoms become the basis for the segregation of the fundamental major plant group units, the classes. A class is the largest, definitely determined, monophyletic group in a subkingdom. A class may be defined, therefore, as: *The largest group of plants in a subkingdom the members of which show an evident relationship to one another as compared with the members of some other group or groups in the same subkingdom.* The emphasis is to be placed on the word "evident," which involves an exercise of judgment by the classifier. Such an exercise of judgment is not required in establishing the seven subkingdoms.

In determining how great or how small a group shall constitute a "class," practical considerations should also have weight. Convenience in delimitation and definition of the group, its practical use in applied science, the advantage in not having too great a number of such units, so that they can be easily retained in the memory, and other similar considerations should be the main criteria in determining the approximate number to be established. The problem is not very different from the one in which a decision is made as to how many large or main branches a given tree with a complex branching system may have. By exercising his own judgment and adopting the work of others the writer has recognized about fifty classes. Some of these classes fall naturally into two or more subclasses and some are so large that a division into subordinate groups, higher than the order, becomes necessary for convenient treatment. These subclasses should also be limited in number for the same reasons as those given for the class. By a reasonable segregation method, the number of classes and subclasses combined falls well below the hundred mark.

With the establishment of the class as the fundamental unit which can be defined quite definitely as to its limits, the systematist has a group which becomes the basis for classification in its broadest aspects. Classes can be compared as to probable relationships and combined into the main branches or *phyla* and *subphyla* on the one hand, and on the other they can be divided into subordinate divisions, the orders.

The Species.

Just as the classes are the units in thinking and treating of plants in their general aspects and in establishing higher groups by combination or lower groups by division, so the species are the units for dealing with plants in their severalty in the science of botany in general and in all the practical relations of life. The species name, whether scientific or common, serves as a means of general communication. The species then must apply to a unit of classification which is both scientific and practical. Too great a refinement of segregation leads to an impossible system for the practical man as well as the botanist who is not especially acquainted with the given group, both because of the impossibility of definite identification and the evident impossibility of keeping a multitude of names in mind based on trivial and wholly unimportant differences. It is not the desire to attempt a definition of species here but simply to make a few practical observations. It soon becomes evident to any one dealing with diverse groups of plants that the concept for specific limits must be different for different groups, not only because of differences in the groups of organisms themselves, but also because of the special practical relations which the members of various groups sustain to mankind. In a general way, the Linnean species make suitable phylogenetic units and the term "species" should be retained for them. A serious attempt should be made to define species in such a way that the term can not be continually shifted to smaller and smaller divisions as is now being done very prominently, especially in some genera. The recognition of smaller units than the species is of great importance in certain lines of study, but definite provision should be made for lower categories within the species to any extent that may be desirable while leaving the larger Linnean units intact.

Many attempts have been made to define a species, but with only partial success. In nonsexual groups, evidently, the species can only be determined and defined by the degrees of morphological and physiological differences, but in the sexual plants, where interbreeding takes place, the species must be established on a different basis. Certainly all the forms that interbreed freely with fertile offspring are to be regarded as belonging to a single species. On the other hand, inability to cross breed is not to be made a basis arbitrarily for species segregation, since we know that there is self sterility of the individual in many groups and often two very closely related varieties may be sterile toward each other.

In classification, the species are to be used as units of comparison in determining the next higher group, the genus. On the other hand, as intimated above, the species may be divided into smaller categories to the extreme degree, ending in the segregation of unit characters. In dividing species into smaller groups, experimental methods are to be employed; in sexual organisms for determining hereditary units, and also for determining fluctuations of ecological variations in both the sexual and the nonsexual. The study of the species resolves itself into genetic analysis on the one hand, and ecological variation or fluctuation on the other. In any freely interbreeding group, the subdivisions of the species are practically all of the same value, but for convenience standard varieties may be established based on some character or set of characters of special practical value, as for instance the consistency of the endosperm which is commonly used for segregating the main varieties of Indian corn, as pop corn, flint corn, sweet corn, etc. These endosperm characters are no more fundamental than various others that might be taken as for example pericarp colors, length of internodes, etc. But such classifications have less value from a practical standpoint. In the subdivision of economic species, therefore, the first consideration should be utility and there is no special reason why this principle should not be carried over to the non-economic species as well, wherever there is free interbreeding.

In taxonomy there are, therefore, two units of special importance, the class and the species. Both of these units must be constantly used in all studies of the evolution and classification of plants on the one hand, and in the practical application of plants in plant industry and the arts, on the other.

Since the species is considered and named in relation to the genus, the genus must also receive due consideration involving both the practical and theoretical sides. A system of names must be devised and established to insure at least a reasonable stability, otherwise the language of botany in so far as it concerns specific names becomes burdensome and even ridiculous. It is remarkable that up to the present time there has not even been developed a system of generic types by which the names could become fairly well stabilized. It is to be hoped that this subject will now receive the serious attention it deserves from systematists.